INTERACTION BETWEEN AN ICHNEUMONID WASP AND THE AUSTRALIAN TONGUE ORCHID IN NEW ZEALAND

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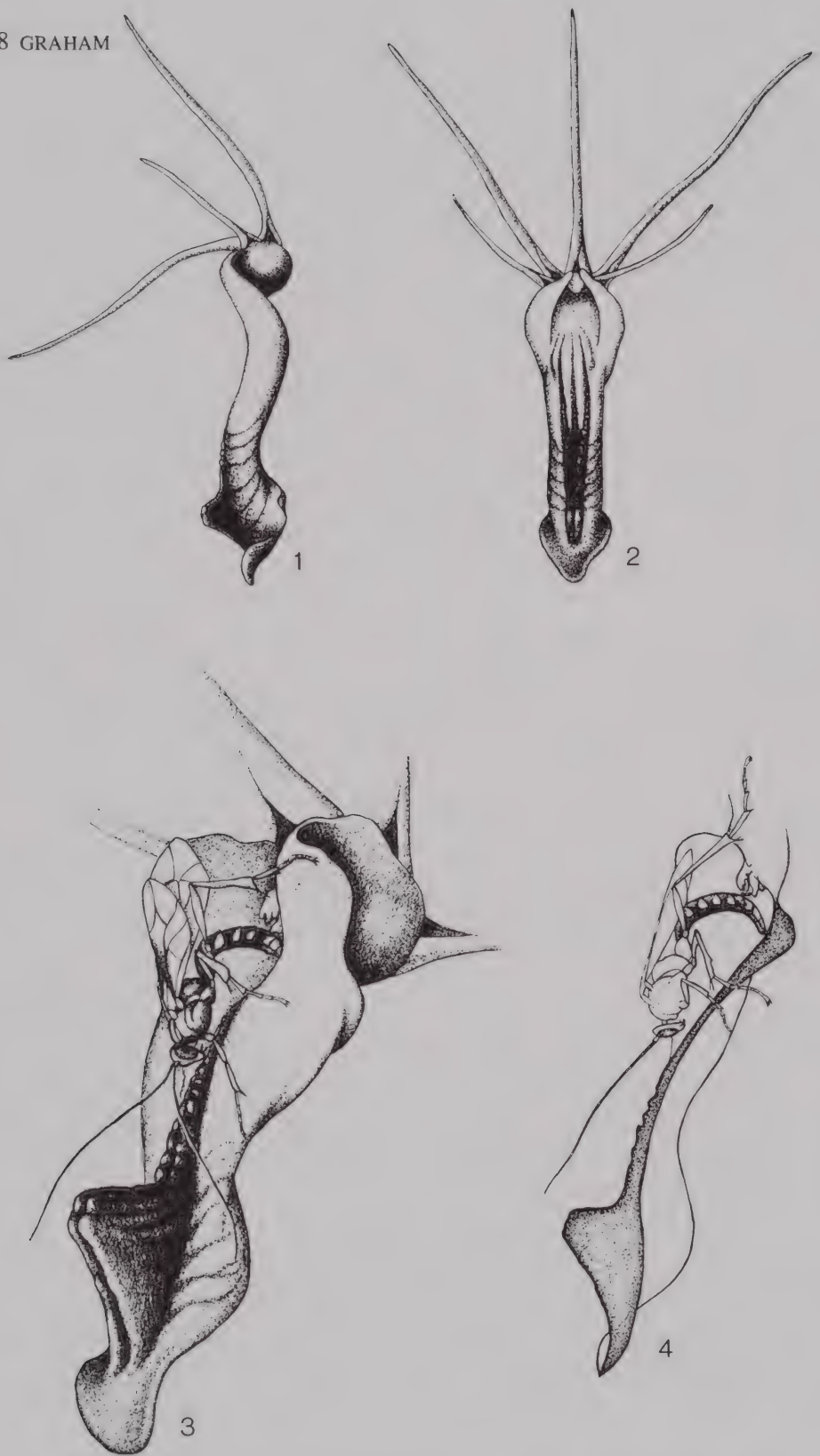
Abstract. Plants of *Cryptostylis subulata* taken from the recently discovered colony in North Auckland were observed during flowering over seven weeks. The only potential pollinators seen in daytime were males of *Lissopimpla excelsa*, a parasitic wasp species long known in many parts of New Zealand. Following pseudocopulation with a flower (as in Australia) the insect carried away waxy pollinia. Most open flowers were visited, often several times, pollinia were removed from 33, but only six capsules matured. Simple experiments indicated that scent was the primary attractant, bringing wasps to newly exposed flowers within 1-2 minutes.

In reporting the discovery at Motutangi Swamp, North Auckland, of the Australian tongue orchid *(Cryptostylis subulata* (Labill.) Reichenb.) Graham (1976) commented "In Australia the flowers of several species of *Cryptostylis* are reputed to mimic the female of an ichneumon wasp *(Lissopimpla semipunctata);* certainly they attract the male wasps which effect pollination. This poses fascinating questions about pollinators and pollination in New Zealand where related wasps occur." Attempts to find answers are reported here.

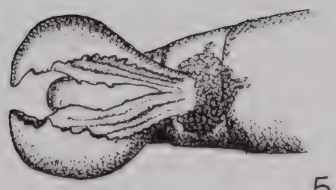
In New Zealand *Lissopimpla excelsa* Costa *(=L.semipunctata* Kirby) [Hymenoptera: Ichneumonidae] is widespread and well known as a parasite of certain subterranean caterpillars. This is the same species that has been often reported to be involved in Australia in sexually conditioned pollination or pseudocopulation with various orchids of the genus *Cryptostylis*. Coleman (1928), following her first report (Coleman 1927), wrote ". . . so, with a Machiavellian cunning almost beyond belief, the orchid lures the artless insect to its service."

The *Cryptostylis* flower has a large reddish labellum *c*.23 mm in length, and long narrow greenish petals and sepals (Figs.1,2); the column, which is described and illustrated by Dockrill (1969), is only 3 mm long, with wings projecting a little above the anther margins, and a very prominent stigma bearing a rounded rostellum. The two-celled anther, standing above the stigma, contains four pollinia, in two lamellate pairs, members of a pair unequal, and all attached directly to a single hemispherical disc. In *C. subulata* flowers are well spaced in a long raceme.

Field observations at Motutangi Swamp (mostly during afternoons) failed to reveal any pollinators though many of the orchid plants bore new and ripening seed capsules. Plants were therefore taken in January 1978 to Whangarei, about 150 km from the only occurrence then known in New Zealand, and five were established in a pot in a garden. The site was open, receiving the sun most of the day and sheltered only from southerly winds. On the hillside below, native forest and manuka *(Leptospermum)* covered a large area, and sections on either side were mostly covered in rank grass. Detailed observations,



Figs. 1-4. 1,2. Flower of *Cryptostylis subulata*. 1. Side. 2. Front. Length of labellum: *c*. 23 mm. 3. Characteristic position of male wasp *(Lissopimpla excelsa)* on flower of tongue orchid *(Cryptostylis subulata)* during pseudocopulation. 4. Orchid flower with part of labellum removed to show position of pollinia in relation to tip of wasp abdomen.



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Figs. 5-7. 5,6. Pollinia attached to wasp abdomen. 5. Dorsal. 6. Lateral. 7. *Lissopimpla excelsa*, female. Length, head to end of ovipositor: *c.* 22mm.

restricted mainly to weekends, continued from late March to mid May. Male ichneumon wasps visiting the flowers were identified by Dr R.P. Macfarlane as *Lissopimpla excelsa* and specimens were deposited in the National Insect Collection at the Mount Albert Research Centre, Auckland. A wasp bearing pollinia firmly attached to the abdomen has been placed in the Auckland Museum, together with colour transparencies of flowers of the tongue orchid.

Observations

Towards the end of March the five plants began to flower and immediately male wasps were attracted. On the morning of 26 March one was seen to fly directly to a flower and attempt to copulate with it. Pale pollinia, 2 mm long, became attached to the wasp's dark abdomen and were easily seen with the naked eye. Between 9.40 a.m. and 3.25 p.m. on that day 13 wasps visited the orchid flowers and at one time five were present.

During the whole period of observation (entirely in daylight hours) no other pollinator was seen, nor were any female wasps detected in the vicinity. Most wasp activity occurred between 8.30 a.m. and noon, after which visits decreased, the latest recorded arrival being at 4.11 p.m. Invariably the number of wasps present was greatest during warm sunny conditions with an accompanying light breeze, and most wasps approached from areas downwind of the orchids.

The wasp usually flies directly to the flower, alighting on the convex surface of the labellum and facing towards the protruding horn near the apex. It then backs rapidly, inserting the tip of its abdomen into the centre of the flower and grasping the outer edges of the labellum with its two long hind legs (Figs.3,4). In this way the end of the abdomen comes in contact with the column, and the viscid disc at the base of the pollinia immediately adheres to it. The abdomen appears to remain almost still but the antennae and wings can move considerably during part or throughout the whole of the pseudocopulation which lasts up to 90 seconds though the average duration is 8 seconds. Out of 40 approaches observed, only five were indirect; twice a wasp alighted on the back of the labellum and three times the head was towards the base of the labellum. All five quickly established the correct position.

The first wasp to visit a recently-opened flower usually detaches itself with the bright yellow pollen masses, of the pollinia glued to the dorsal surface of the abdomen (Figs.5,6), presumably in position for touching the stigma of the next flower. The wasp may fly off to another flower, or it may re-enter the same one, repeating pseudocopulation up to 19 times before leaving. A wasp visiting a series of fresh flowers can become festooned with the pollinia from four or five flowers, without any apparent effect on its flying ability. On two occasions when only one fresh flower was available the wasp that removed the pollinia returned after an hour's absence with pollinia still attached. Very rarely were as many as three flowers open at a time on any one stem and it was not uncommon, when numerous wasps were present, to see two or even up to five of various sizes 'copulating' simultaneously with one flower. Flowers from which pollinia had not been taken lasted 14 to 16 days, in observed cases. A flower without its pollinia may be visited by wasps for some hours but its attractiveness soon diminishes. There was no evidence of feeding or of deliberately gathering pollen.

The five plants bore a total of 73 flowers, of which 33 had the pollinia removed by wasps, but only six capsules developed. Fertilisation was achieved only in flowers near the base of each raceme, namely the first, third and fourth out of 14, the first and third out of 20, and the fifth out of 14.

Experiments

The strong attraction that the fresh orchid flower exerts on the male ichneumon wasp appears to be due to an odour that human senses do not perceive. Two simple experiments confirmed that scent is the primary attractant.

First, the plants were moved indoors so that flowers opened away from wasps. After five days the plants, now bearing fresh flowers, were placed outside again. Within 45 seconds the first wasp arrived, and after two minutes five were in attendance; all came from downwind of the orchids, suggesting a strong scent attractant.

Subsequently, the orchids were taken indoors for a further five days, then placed outside again, this time with the entire plant covered with a fine muslin cloth. The results were much the same, with the first wasp coming 73 seconds after the shrouded plants were put out. This wasp flew almost directly to the base of the covering and gained immediate access to the flowers. All the seven other wasps that were seen to arrive were able to reach the hidden flowers without too much searching. In two other sites to which the orchids were transferred similar trials gave comparable results.

Discussion

Modern work on chemical attractants in pollination is reviewed by Faegri & van der Pijl (1966) and by Proctor & Yeo (1973) who also refer to visual and tactile stimuli. The phenomenon of pseudocopulation in which male insects perform at least part of the mating behaviour in response to orchid flowers has long been known (Correvon & Pouyanne 1916) and the relationship between species of *Lissopimpla* and of *Cryptostylis* in Australia is extensively documented (Coleman 1927-1938; Froggatt 1927; Godfrey 1929; Leonard 1970; Stoutamire 1974, 1975; Bates 1977; Wallace 1978).

The flower of *Cryptostylis subulata* resembles the female *Lissopimpla* wasp in certain superficial respects, perhaps sufficiently to orient the male wasp into the correct position to pick up the pollinia. By comparing the female wasp (Fig.7) with the anterior view of the flower (Fig.2) some similarities can be recognized. The two outer calloused ridges and the dark central line that traverses most of the length of the labellum, with their highly polished surfaces, could simulate the pattern of white dots down the sides of the female's abdomen, and also closely parallel the tactile quality of the wasp's body. The silhouette created by these three dark lines has a vague approximation to the abdomen with ovipositor and the long hind legs of the female. The fine but distinct veining that extends out horizontally from the central ridge and down the tightly reflexed mid section of the labellum may enhance the overall resemblance. Visual or tactile stimuli may play a part but it was noticed that flowers, though otherwise unchanged, seemed to lose their attractiveness soon after pollinia had been removed.

The observations now reported show that the male wasps of *L. excelsa* are immediately attracted by scent to flowers of the tongue orchid, a plant with which, in New Zealand, they can have had no previous experience. The numbers of wasps competing (on most days) for the available flowers ensured that nearly all open flowers would be visited at least once but fewer than ten per cent developed into capsules. The wasps carried away pollinia, sometimes collecting several sets from different flowers, but deposition of pollen on stigmas was not observed. The waxy pollinia appeared to remain intact on the insects' bodies, but gradual attrition might perhaps have occurred, with granules being left on stigmas (compare Darwin 1877).

The *Cryptostylis/Lissopimpla* example is often quoted in discussions of the important reciprocating evolutionary processes underlying plant/animal interactions but such theoretical considerations lie outside the scope of this paper.

Acknowledgements. The author expresses thanks to L.B. Moore, R.P. Macfarlane, and E.W. Valentine for constructive help; also to Mr and Mrs R. Seymour for continuing interest and assistance, and to Susan Graham who succeeded in capturing the female wasp depicted.

[Digby Graham died on 18 March 1979. In the previous October the draft of his paper was considered by L.B.M., R.P.M., and E.W.V. The present version, belatedly edited by L.B.M., incorporates information added in response to queries arising from his first draft. In the list of References those marked *, considered by an anonymous referee to be important, were not mentioned in the original text; most are brief and some later ones were not available to the author during his study. Stoutamire (1974, 1975) presented evidence of self-incompatibility in *Cryptostylis*, and Wallace (1978) noted that the flowering of *Cryptostylis* coincides with the activity of male *Lissopimpla* which emerge from pupation some time before the females.]

[The Seymours have sighted and photographed Ichneumonid wasps pseudocopulating with Australian tongue orchid flowers *in situ* at Motutangi Swamp during the mornings (but not the afternoons) of 5, 6 November 1983. — Editor]

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